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Spotlight

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# Hot n' Cold: Molecular Signatures of Domestication Bring Fresh Insights into Environmental Adaptation

Recent investigations of divergent rice genotypes have identified previously unknown molecular adaptations conferring heat and chilling tolerance in their corresponding local environments (Figure 1). These studies shed new light both on the domestication of rice and environmental adaptation strategies.

Plants are inevitably exposed to temperature fluctuations throughout their life cycle. Although plants have the ability to adapt to short-term changes in temperature, long-term exposure to extreme changes such as heat or freezing have dire consequences for the health of the plant. They must adapt to these changes to survive and reproduce. Precisely how plants respond and adapt to these temperature fluctuations within the cell is largely unknown. Understanding the mechanism and applying the knowledge could hold the key to sustaining and improving crop yields as climate change takes hold. Rice offers an amazingly rich genetic resource for understanding environmental adaptation, thanks to several independent domestication events under different climatic conditions (Huang et al., 2012; Purugganan, 2014). Exploitation of this diversity has led to the genetic dissection of important agronomic traits (Huang et al., 2011; Mickelbart et al., 2015). Here, we discuss recent advances in understanding the adaptation of rice to high and low temperatures (Li et al., 2015; Ma et al., 2015) that could help mitigate the effects of climate change on major crop species such as rice.

## CLEARING OUT THE BAD APPLES: A NEW PARADIGM FOR DEALING WITH HEAT

High temperatures result in the loss of structure and function of proteins, which then aggregate and disrupt cellular processes. Successful stress adaptation relies on the ability of the cells to maintain protein homeostasis and minimize cellular damage. In a landmark study, Li et al. (2015) showed that enhanced 26S proteasome function enables thermotolerance in rice. African rice (*Oryza glabberima*), which was domesticated independently (Callaway, 2014), is highly heat tolerant compared with its Asian counterpart (*Oryza sativa* spp. *japonica*). Li et al. identified *Thermo-tolerance 1* (*TT1*) as the major quantitative trait locus (QTL) underlying thermotolerance in *O. glaberrima*. *TT1* encodes the $\alpha 2$ subunit of the 26S proteasome, which degrades ubiquitinated proteins (Vierstra, 2009). The finding of TT1 as a proteasome component therefore implicates protein degradation as an important mechanism for thermotolerance. Consistent with this, Li et al. (2015) found that *OgTT1*, the dominant allele in *O. glaberrima*, leads to thermotolerance through efficient removal of cytotoxic ubiquitinated proteins. Remarkably, allelic variation of *TT1* was associated with geographical distribution, providing evidence that *TT1* is specifically selected for local adaptation. Ultimately the study shows that enhancing TT1 function can lead to increased thermotolerance both in other rice varieties and other plant species.

The 26S proteasome is a central part of the ubiquitin-proteasome system, which is responsible for maintaining proteomic plasticity underlying growth, development, and environmental adaptation in plants (Vierstra, 2009). The implication of this proteasome in the regulation of heat-stress tolerance and adaptation to the local environment in rice by Li et al. (2015) offers a fresh perspective on high temperature adaptation in plants that further underscores its significance. Heat-shock protein-mediated protein homoeostasis through refolding denatured proteins to maintain their structure within the cytoplasm is considered the major mechanism for thermotolerance (Vierling, 1991). Crucially, this elegant and comprehensive study suggests that removal, rather than functional recovery, of denatured proteins is both necessary and sufficient for tolerance to prolonged exposure to heat.

## FEELING COLD

Similarly to heat adaptation, plants must sense dangerously low temperatures and initiate signaling cascades to ensure effective cellular acclimatization to cold. Despite the current understanding of major molecular components in cold adaptation, a mechanistic framework of low-temperature adaptation remains elusive. The *indica* and *japonica* subspecies of cultivated rice *O. sativa* have clearly diverged as a result of domestication and breeding to suit their respective geographical locations. The latter shows enhanced growth and survival in colder climates. While it is known that the ability to adapt to low temperatures constrains geographical distribution, key factors that underlie success in cold-adapted plants and evolution in such climates are not known.

In a study complementary to that discussed above, *COLD1* (*Chilling tOLerance Divergence1*) was recently discovered as a major QTL for cold adaptation by analyzing recombinant inbred lines from a cross between cold-tolerant *japonica* (Nipponbare) and cold-sensitive *indica* (93-11) (Ma et al., 2015). $COLD1^{jap}$

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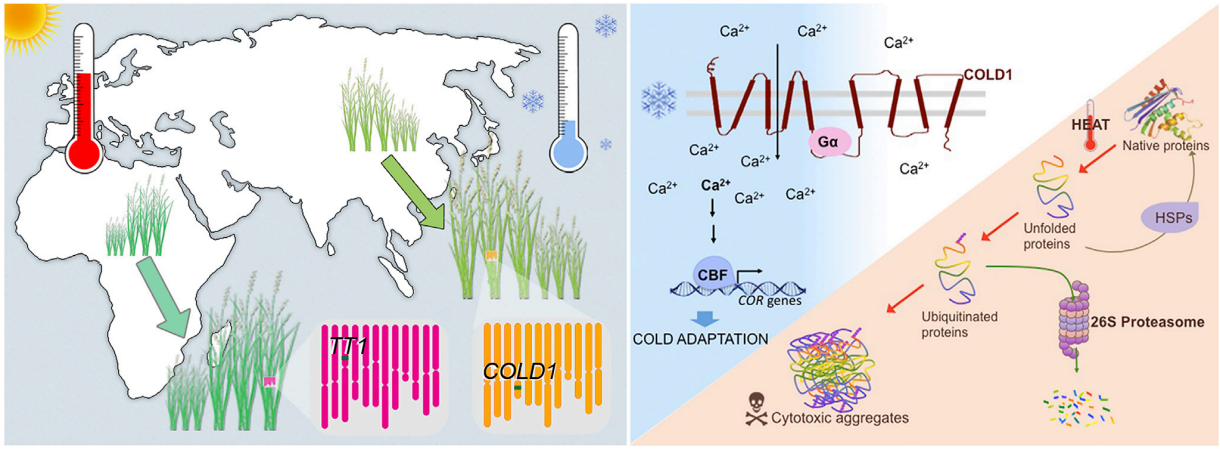


**Figure 1. Fresh Mechanistic Insights into Temperature Adaptation in Rice.**
Facilitated by advances in genetics, two exciting recent studies unveiled QTLs from geographically isolated rice populations that are crucial for tolerating extreme temperatures. *COLD1*, isolated from Asian rice *Oryza sativa* spp. *japonica*, interacts with rice G protein α subunit 1 to regulate cold-induced $Ca^{2+}$ signaling. *TT1* from African rice *Oryza glabberima* encodes the α subunit of rice's 26S proteasome. This landmark discovery revealed a new model whereby removal of denatured, aggregated proteins can determine a plant's tolerance to heat rather than recovery of their function.

contained a single-nucleotide polymorphism that was shown to have its origins in *Oryza rufipogon* (Chinese wild rice), which was selected during the domestication of *japonica* rice. Localized to endoplasmic reticulum and plasma membrane, COLD1 was found to interact with rice G-protein α subunit 1 (RGA1).

Heterotrimeric guanine nucleotide-binding proteins (G proteins) act as molecular switches to initiate signaling cascades. G-protein complexes function in extracellular signal perception and responses through interactions with and regulation of ion channels (e.g. $Ca^{2+}$ channels) in mammals. In plants they are involved in growth and development as well as environmental responses (Urano and Jones, 2014). Although $Ca^{2+}$ has been implicated in low-temperature adaptation in plants, how changing temperatures regulate movement of this ion remains unknown. Ma et al. (2015) showed that COLD1 accelerates GTPase activity and leads to cold-induced calcium ($Ca^{2+}$) influx. $COLD1^{jap}$ proved more effective in stimulating RGA1 than its *indica* counterpart. Consistent with a potential role of COLD1 in sensing the cold signal, $COLD1^{jap}$ leads to stronger activation of cold-responsive genes such as *OsDREB*s.

G proteins have been implicated in other traits through their interaction with the key regulators (Urano and Jones, 2014). These appear to act as major modules to integrate environmental signals. Depending on the nature of the external cue, downstream signaling is initiated to acclimatize to changing environments through the action of hormones and other systemic signals.

The elegant studies of Ma et al. (2015) and Li et al. (2015) illuminate molecular frameworks of high- and low-temperature adaptations in rice, and for plants in general. They also raise exciting new questions to be addressed, such as how the 26S proteasome is regulated by heat. While they found that *TT1* expression increases at higher temperatures, increasing TT1 (the α2 subunit) or having a hyperactive allele was sufficient to enhance thermotolerance. Understanding what facilitates this would further illuminate upstream regulatory steps of temperature perception.

Regulation of cold tolerance by *COLD1* through altering the GTPase activity of the rice G-protein α subunit is an exciting new paradigm. How low temperature regulates COLD1 function in other systems remains to be seen. Molecular understanding of COLD1-mediated $Ca^{2+}$ flux and its role in cold tolerance would be critical for defining a comprehensive framework underpinning temperature adaptation. Individually, the studies on *TT1* and *COLD1* showed that these proteins were critical for adaptation to specific geographical regions and were selected for during domestication. Together, one interesting aspect will be to address the co-evolutionary perspectives of *TT1* and *COLD1* and whether selection (natural or artificial) of one would influence the other.

Further research into the molecular and evolutionary aspects of *TT1* and *COLD1* are sure to illuminate plant environmental responses in years to come. Such a fine understanding would indeed be highly valuable in developing crops that adapt to a changing climate.

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## REFERENCES

**Callaway, E.** (2014). Domestication: the birth of rice. Nature **514**:S58–S59.

**Huang, X., Zhao, Y., Wei, X., Li, C., Wang, A., Zhao, Q., Li, W., Guo, Y., Deng, L., Zhu, C., et al.** (2011). Genome-wide association study of flowering time and grain yield traits in a worldwide collection of rice germplasm. Nat. Genet. **44**:32–39.

**Huang, X., Kurata, N., Wei, X., Wang, Z.-X., Wang, A., Zhao, Q., Zhao, Y., Liu, K., Lu, H., Li, W., et al.** (2012). A map of rice genome variation reveals the origin of cultivated rice. Nature **490**:497–501.

**Li, X.-M., Chao, D.-Y., Wu, Y., Huang, X., Chen, K., Cui, L.-G., Su, L., Ye, W.-W., Chen, H., Chen, H.-C., et al.** (2015). Natural alleles of a proteasome $\alpha 2$ subunit gene contribute to thermotolerance and adaptation of African rice. Nat. Genet. **47**:827–833.

**Ma, Y., Dai, X., Xu, Y., Luo, W., Zheng, X., Zeng, D., Pan, Y., Lin, X., Liu, H., Zhang, D., et al.** (2015). COLD1 confers chilling tolerance in rice. Cell **160**:1209–1221.

**Mickelbart, M.V., Hasegawa, P.M., and Bailey-Serres, J.** (2015). Genetic mechanisms of abiotic stress tolerance that translate to crop yield stability. Nat. Rev. Genet. **16**:237–251.

**Purugganan, M.D.** (2014). An evolutionary genomic tale of two rice species. Nat. Genet. **46**:931–932.

**Urano, D., and Jones, A.M.** (2014). Heterotrimeric G protein-coupled signaling in plants. Annu. Rev. Plant Biol. **65**:365–384.

**Vierling, E.** (1991). The roles of heat shock proteins in plants. Annu. Rev. Plant Physiol. Plant Mol. Biol. **42**:579–620.

**Vierstra, R.D.** (2009). The ubiquitin-26S proteasome system at the nexus of plant biology. Nat. Rev. Mol. Cell Biol. **10**:385–397.